

The University of Chicago

NUTRITIONAL LEVELS IN THE PEANUT PLANT

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF BOTANY

1936

By

RUFUS HENRY MOORE

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NUTRITIONAL LEVELS IN THE PEANUT PLANT
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 477

RUFUS H. MOORE

(WITH TWO FIGURES)

Introduction

PETTIT (12) has discussed the morphology, growth responses, and reproduction of the peanut plant. WALDRON (23) added information concerning the general morphology and physiological response. In both papers the plant is considered indigenous to Brazil, and other species of the Leguminosae which form at least part of their fruits below the surface of the soil are described. REED (17) emphasized the developmental morphology of the fibrovascular bundle, gametophyte, and embryo. Recently STOKES and HULL (19) and HUSTED (4) have reported upon the genetics and cytology of cultivated varieties.

Investigation

The present investigation concerns the responses of the peanut plant to the variations in the supply of light and available nitrogen it may receive. More specifically the planes of nutrition were varied in order to produce definite type responses as follows: (1) complete suppression of reproductive activity, induced by an abundant supply of readily available nitrogen and a very limited accumulation of carbohydrates; (2) production of flowers and gynophores, but not of fruits, induced by an abundant supply of less readily available nitrogen and a slightly increased accumulation of carbohydrates; (3) an abundance of flowers, gynophores, and fruits, induced by a reduction in the supply of available nitrogen and an increased accumulation of carbohydrates; (4) production of flowers and gynophores but not of fruits, induced by a much restricted supply of available nitrogen and a further accumulation of carbohydrates; and (5) complete suppression of reproductive response, induced by still greater restriction of available nitrogen and a still greater accumulation of carbohydrates.

Essentially these five type responses were secured in the cultural treatments summarized in table 1.

Seed of the Spanish variety, strain 18-38-M-9, selected for thirteen successive generations by the United States Department of Agriculture, was secured. To insure freedom from disease organisms and nodule-forming bacteria, bright and unbroken pods were treated with a 0.25 per cent solution of Uspulun for three successive half-hour periods. As soon as the pods were sensibly dry the seeds were shelled. Seeds were used only from pods which had remained dry inside during the treatment.

TABLE 1
TYPE RESPONSES IN RELATION TO CULTURAL TREATMENTS

TYPE RESPONSE	CULTURAL TREATMENTS			
	SERIES	SOURCE OF NITROGEN	LENGTH OF DAY	NUMBER OF PLANTS
1.....	A	NH ₄	6 hours	48
2.....	AA	NH ₄	Seasonal	12
2.....	B	NO ₃	8 hours	48
3.....	C	NO ₃ and NH ₄	Seasonal	48
4.....	D	NO ₃	Seasonal	48
5.....	E	None	Seasonal	48

NUTRIENT SOLUTIONS.—Certain modifications of the more or less standard nutrient solutions were necessary or useful. Seedling peanut plants were found to require a minimum concentration of calcium salts of 0.0006 gm. mols per liter.¹ Healthier and more vigorous seedlings were produced by using ammonium nitrogen than nitrate nitrogen (9). Concentrations of the phosphate ion ordinarily used in nutrient solutions were found to be injurious to the plant when grown in the light; those grown in darkness are not subject to phosphate toxicity. It was found possible to apply the ammonium nitrogen nutrient solution from a single siphon in drip-culture by reducing the concentrations of the calcium and phosphate ions.

GENERAL REPRODUCTIVE BEHAVIOR.—Under the conditions of light and temperature prevailing in Chicago during the spring, the

¹ Reference to the concentrations of salts in nutrient solutions will always be made on this basis.

peanut plant begins to bloom from four to six weeks after planting. The pre-blooming stage can be extended a week or more by the use of ammonium nitrogen.

From one to eight sessile flowers form in the axil of each leaf. These usually open early in the morning, pollination occurs, and the petals generally begin to wither before the day is over. Thus it is possible to make accurate counts of the number of flowers produced. After several days, the fruit stalk or gynophore begins to elongate noticeably, the dried remains of the floral envelope and included organs often capping the ovary. Elongation of the gynophore is initiated by cells at the base of the ovary (12). The meristem formed here persists until the ovary is pushed a few centimeters below the surface of the soil, or in case the substratum is not reached, until the gynophore is 10 to 15 cm. in length. During the growth of the gynophore the ovary does not increase perceptibly in size. Usually it does not begin to enlarge until it has been buried in the substratum.

The period between the opening of a flower and the beginning of elongation of its gynophore will be referred to as the flower-to-gynophore interval. Data for plants grown in 1933 are summarized in table 2.

RESPONSES TO PHOTOPERIOD AND AVAILABLE NITROGEN.—The peanut, like the tomato, was found to be an indeterminate bloomer. A jar of six plants blossomed abundantly when continuously illuminated for several weeks. Other plants subjected to three- or four-hour periods of daylight under a muslin canopy blossomed sparingly, until approaching exhaustion of their carbohydrates induced progressive death of leaves.

Responses to available nitrogen were studied in 1933 and 1935. In 1933 four series of plants were grown without shading (table 2). Although the concentration of $\text{Ca}(\text{NO}_3)_2$ supplied to the several series varied over a wide range, all plants were fruitful. Vegetative extension and the size of the crop of fruit were directly correlated with the available nitrogen given. Chemical analyses were made on oven-dried tissues (6, 7) of only the highest and lowest nitrogen series. Chemical data are of some interest (table 3), as the plants were dissected into a greater number of fractions than they were for the analyses of 1935 (tables 6-9).

CULTURE OF PLANTS FOR MAIN PROBLEM

To grow plants representing the five type responses chosen, the following experiments were conducted in 1935.

All plants received the same treatment from the time of seeding until the specific cultural treatments were begun. On April 12, treated seeds were sown thickly in white quartz sand which had been put into glazed 3-gallon jars, washed with an acid solution, flushed

TABLE 2
FLOWER-TO-GYNOPHORE INTERVAL (1933)

SERIES	CONCENTRATION OF $\text{Ca}(\text{NO}_3)_2$	FLOWERS PRODUCING GYNOPHORES		FLOWER-TO-GYNOPHORE INTERVAL IN DAYS	
	GRAMS MOLES PER LITER	NUMBER*	ANTHESIS	AVERAGE	MODE
High nitrogen.....	0.01500	108	July 16-31	12.7	7
		156	Aug. 1-23	8.8	7
Medium nitrogen.....	0.00450	190	July 16-31	17.0	9
		314	Aug. 1-23	11.0	9
Low nitrogen.....	0.00225	64	July 16-31	16.4	9
		148	Aug. 1-23	10.9	9
Very low nitrogen....	0.00113	61	July 16-31	11.3	9
	0.00032	None	Aug. 1-23		

* Totals for four plants from each series.

with distilled water, sterilized in an autoclave, and held at 28°C. during germination. Four days later, when the cotyledons were just emerging, six seedlings as nearly uniform as possible in appearance were transplanted to each jar containing sand prepared as indicated for experimentation. To stimulate vegetative growth, nutrient solution I (table 4) was applied daily for two weeks. On April 26, solution II was substituted and the concentration of its salts was doubled at the end of a week. Manganese, as MnSO_4 , was applied at about 0.4 p.p.m. and boron, as H_3BO_3 , was applied at about 0.3 p.p.m., each time nutrient solutions were given. Iron, as FeCl_3 , was applied once or twice weekly at the rate of 1-2 p.p.m. for series showing

little vegetative growth and at 5 p.p.m. for those showing extensive growth.

Because of the early onset of blossoming, specific cultural treatments were established when the plants were a little less than four weeks old. At that time the plants were healthy and vigorously

TABLE 3
SUMMARY OF CHEMICAL ANALYSES OF HIGH AND
VERY LOW NITROGEN SERIES (1933)*

SERIES	FI- BROUS ROOTS	PRI- MARY ROOTS AND HYPO- COT- YLS	STEMS	STEM TIPS	PETI- OLE	LEAF- LETS	FLOW- ER- BUD COM- POSITE	GYNOPHORES		FRUITS		
								NON- FRUIT- ING	FRUIT BEAR- ING	SMALL	LARGE	
											SHELLS	SEEDS
High N. Very low N. .	Total sugars											
	2.16 8.76	4.09 7.62	5.13 4.95	1.53 2.17	1.53 1.25	1.12 1.59	2.34 2.27	1.65 1.83	3.79 3.47	11.16 8.92	10.73 11.66	2.87 5.04
	Starch and dextrins											
	0.37 1.99	7.01 11.86	7.77 7.89	2.81 7.97	1.64 10.66	6.01 26.23	5.03 6.16	9.00 5.98	17.60 8.14	10.03 17.66	2.94 2.83	8.52 15.32
	Total sugars, starch, and dextrins											
High N. Very low N. .	2.53 10.75	11.10 19.48	12.00 12.84	4.34 10.14	3.17 11.91	7.13 27.82	7.37 8.43	10.65 7.81	21.39 11.61	21.19 25.98	13.67 14.49	11.39 20.36
	Ether extract											
								1.33 1.45	0.73 0.85	1.40 2.45	0.59 trace	44.96 47.02
	Total nitrogen plus nitrates											
	High N. Very low N. .	1.82 1.52	1.20 0.70	1.07 0.64	4.51 1.47	1.57 1.01	3.38 1.74	2.70 1.70	3.11 2.30	1.97 1.39	5.36 3.96	1.89 0.93

* All figures are for percentages of dry weight. Analytical methods were the same as for 1935 except that total nitrogen plus nitrates were determined by the salicylic acid method.

vegetative, each having seven to nine fully expanded leaves. To avoid the complication of fruit setting before the plants in series A, B, D, and E had reached the desired level of nutrition, flower buds or freshly opened flowers were removed for a time. Daily counts were taken of all flower buds or flowers produced whether or not these

were removed or allowed to remain on the plants. Gynophores were counted periodically in the preceding four series.

SERIES A: VERY HIGH NITROGEN, NON-FRUITFUL.—Each jar of this series was given nutrient solution A, continuously supplied (21) from one siphon. The solution was collected in 18-liter carboys as it drained from the jars, the pH of 7.1 restored with dilute NH_4OH , and the solution used again. Every seven to nine days the jars were thoroughly flushed with tap water, fresh nutrient solution allowed

TABLE 4
NUTRIENT SOLUTIONS

NUTRIENT SOLUTION	CONCENTRATION OF SALTS (GM. MOLS PER LITER)							PH AT APPLI- CATION
	(NH ₄) ₂ SO ₄	NH ₄ NO ₃	CaCl ₂	Ca(NO ₃) ₂	KH ₂ PO ₄	KCL	MgSO ₄	
I.	0.00010		0.00090		0.000225	0.000225	0.00045	6.9
II.	0.00040		0.00040	0.00040	0.000045	0.00060	0.00060	
A.	0.0060		0.00225		0.001125	0.0030	0.0030	7.1
AA.	0.0090		0.00225		0.001125	0.0030	0.0030	7.3
B.				0.0090	0.001125	0.0030	0.0045	4.5
C-I.				0.0045	0.001125	0.0030	0.0045	4.0
C-II.		0.00079	0.00079	0.00315	0.001125	0.0030	0.0030	5.3
DE.			0.00180		0.000090	0.00180	0.00180	4.3
High N, 1933				0.01500	0.002250	0.002250	0.00450	4.1
Very low N, 1933*				0.00032	0.000080	0.000080	0.00016	4.1

* Formula for the nutrient solution used beginning August 1.

to drain through the sand, and the supply carboys filled with fresh nutrient solution for the next period. During the seven- to nine-day periods of repeated use of the nutrient solution, about 3 per cent of the ammonium nitrogen was daily oxidized to nitrate nitrogen.

The plants were given a six-hour day, from 8:30 A.M. to 2:30 P.M. Light intensity was reduced by muslin stretched 4 feet above the plants. During heavily clouded weather the canopy was rolled up. On very bright days it was supplemented with one or two layers of longcloth.

SERIES AA: VERY HIGH NITROGEN, LIMITED FRUITFULNESS.—Only two jars of plants were included in this test. Nutrient solution AA was supplied by the continuous application method used for

series A. Originally the former series was intended as a guide to determine whether the concentration of 0.0060 for $(\text{NH}_4)_2\text{SO}_4$ planned for series A would be toxic. As the plants remained healthy the test was continued.

The plants were shaded by muslin about 1 foot above the rim of the jars and were exposed to the seasonal length of day. Muslin protected the plants from direct sunlight during the early morning and late afternoon.

SERIES B: HIGH NITROGEN, LIMITED FRUITFULNESS.—This series received nutrient solution B. The plants were moved out of the

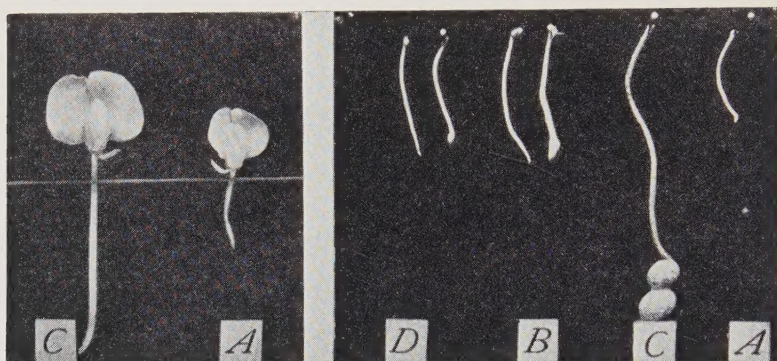


FIG. 1.—Flowers and gynophores produced in the several cultures: C, abundantly fruitful; A, very high nitrogen, non-fruitful; D, high carbohydrate; B, high nitrogen, limited fruitfulness.

dark house at 8:30 A.M. and back into it at 4:30 P.M., thus giving them an eight-hour day. Light intensities were greater than for series A, and were varied in a similar manner.

In this series the size of the flowers was used as an index to the nutritional level of the plants. It had been noticed that plants with a very limited accumulation of carbohydrates produced flowers about half as large as those on plants of only slightly greater carbohydrate reserve (fig. 1). Accordingly the nutrient solution and intensity of light were varied to maintain, as far as possible, the production of flowers of reduced size.

SERIES C: ABUNDANTLY FRUITFUL.—When the plants of this series were one month old, they were thinned to four per jar. Nutrient solution C-I was applied during the succeeding two and one-half

weeks, and solution C-II during the remainder of the experimental period. The concentration and quantity of nutrient solution were varied as necessary to maintain abundant production of flowers and gynophores. The plants were given full exposure to daylight.

SERIES D AND E: HIGH CARBOHYDRATE.—Both series were given the same treatment, except for slight variations noted hereafter. At the start of the treatments all nitrogenous salts were flushed from the sand with distilled water and nutrient solution DE. The concentrations of salts in this solution were very low, as ordinary concentrations had been found to be injurious and it was necessary to apply the solutions three times per week to stabilize the pH. Previous observations on high carbohydrate plants had shown that they soon accumulate ions to the point of toxicity, one of the most serious effects being the failure of such plants to accumulate any considerable amount of starch. When visible growth of the plants in these two series had practically ceased (June 9), the concentrations of all salts except KH_2PO_4 were reduced to one-half that recorded for them in table 4 in order to minimize possible injurious effects.

No nitrogen was added at any time to the nutrient solution of series E. Small amounts of nitrate were added to series D when it seemed that flower production was about to cease. Between June 22 and July 19, 8 liters of nutrient solution DE with $\text{Ca}(\text{NO}_3)_2$ at a concentration of 0.0001125 and 3 liters with this salt at a concentration of 0.000225 were added to each jar. Both series were exposed to the greatest available amount of direct sunlight.

In these series, as in series B, the size of the flowers was used as a criterion of nutritional level. About the time the lower leaves began to turn bright yellow and drop, the flowers became periodically much reduced in size and paler in color. Exfloration was discontinued in series D during the second cycle of floral reduction, and in series E during the third.

CONTROL OF pH.—On an average of once every two weeks, the pH of each jar in series B, C, D, and E was taken. At such times nutrient solution was applied to the cultures and the first 50 to 100 cc. of drip collected. All determinations were made by use of indicators on 2–3 cc. samples.

After determinations had been made, the pH was adjusted if nec-

essary with 0.001 N KOH or 0.006 N H_2SO_4 . One or 2 liters of base or acid were added, followed by sufficient distilled water and nutrient solution to flush the sand. Table 5 summarizes the pH determinations.

It must be emphasized that each series was grown to secure a definite type response. Cultural treatment could not be a matter of inflexible routine therefore, for light, temperature, and relative humidity, which depend largely upon weather conditions, varied over a rather wide range. Accordingly it was necessary to modify cultural practice in order to produce the type responses desired.

TABLE 5
SUMMARY OF AVERAGE PH DETERMINATIONS

pH OF NUTRIENT SOLUTION	SERIES					
	CONTINUOUS APPLICATION		PERIODIC APPLICATION			
	A	AA	B	C	D	E
Applied	7.1	7.3	4.0	5.2	4.3	4.3
Drip	5.5	5.5				
First drip before flushing			5.0	5.7	4.8	5.1
Mean deviation of jars			± 0.43	± 0.28	± 0.60	± 0.34

COMPARATIVE CULTURES OF TOMATO.—For comparison a few tomato plants were included with each of the preceding treatments except AA. Two plants of the Marglobe variety were grown per jar, two jars having been included with series A and E and one with series B, C, and D. The number of plants used was limited.

CHEMICAL METHODS

HARVEST AND PRESERVATION.—An abundance of sunshine favored the accumulation of carbohydrates toward the close of the experiment. Records of the weather bureau at the University of Chicago show that, for the eleven days preceding the first day of harvest, there was a daily average of 11.8 hours of sunshine.

Harvesting was done from July 19 to 21. In all cases the plants were placed in the dark house overnight. The following morning

each series was removed just before dissection, carefully flushed from the jars, and sand adhering to the roots and fruits dislodged with a jet of tap water.

Dissections were made at once in the laboratory. All series were separated into root, stem, petiole, leaflet, and composite fractions. Hypocotyls were included with roots. The stem fraction consisted of all stem tissue save that of the youngest 2 cm., the stem tips. Only healthy leaflets were used in the leaflet fraction, the remainder of such healthy leaves comprising the petiolar fraction. The composite fraction consisted of all leaves that were discolored in any way, stem tips, axillary buds, and (in the cases of all series except B and C) the gynophores. The fruits of series B were too small and few to constitute a separate fraction, and hence were combined with the gynophores to make a single fraction. The gynophore fraction of series C contained not only gynophores which had not reached the sand, but also those with very slightly enlarged ovaries. The fruit fraction of series C included both the fruits proper and the gynophores on which they had formed. Only the stems of the tomato plants were harvested.

The fractions were minced, preserved in 80 per cent alcohol by standard procedure, and stored in the dark. About two hours elapsed from the time series C was flushed from the jars until the fractions were put into alcohol. The period of harvest for the other series averaged about one hour. Extractions were made during the two succeeding weeks by standard procedure (2), except that Schleicher and Schüll filter paper no. 595 was used instead of hardened filter paper, to facilitate the rate of filtration. Filtrates were brought to volume and aliquoted at 25°C. All filtrates were free from cloudiness except that of the fruits in series C, which had a fine and somewhat stable suspension that appeared oily in nature. The ether extract of this filtrate appears in table 8. The residues of alcoholic extraction were ground first in a drug mill and then for twelve hours in a ball mill, dried in a vacuum oven at 80°, and stored in desiccators.

CARBOHYDRATES.—Copper precipitations were made by the QUISUMBING-THOMAS method (16) and the copper determined by the volumetric permanganate method of the A.O.A.C. (1).

SUGARS.—Sugar determinations were made on 500 cc. aliquots of filtrates prepared for analysis as described by STUART (20). Analyses were made for total sugars on 110 cc. of the cleared filtrates. The solutions were made just acid to methyl red with 10 per cent acetic acid. Two drops of Difco invertase solution were added and the reducing power was determined after three hours of enzymatic action at 37°. Total sugars are expressed as invert sugars. Reducing sugars were determined only on the stems.

STARCH AND DEXTRINS.—Beakers of 250 cc. capacity covered with sections of petri dishes were used for gelatinization and digestion. Samples of the dried residues were taken up with about 20 cc. of distilled water and gelatinized by heating on a steam bath and for 45 minutes in an 80° oven. After cooling, 4 cc. of fresh saliva was added and the samples digested for 45 minutes at 37°. The digested samples were heated over a steam bath, filtered hot, and washed free from sugars. Sufficient HCl was added to the filtrates to produce an acid concentration of 2.5 per cent, and the samples refluxed in boiling water for two and one-half hours. After cooling, they were made alkaline to methyl red but just acid to litmus paper. Results are expressed as starch, using 0.93 as the factor.

“HEMICELLULOSES.”—The residues from which starch and dextrans had been removed were taken up in 2.5 per cent HCl, refluxed for two and one-half hours in boiling water, filtered, and cleared before analyses. Results are expressed as dextrose.

SOLUBLE NITROGEN.—Analyses were made on 100 cc. portions of the alcoholic extract by the reduced iron method (15).

INORGANIC NITROGEN.—The methods of STUART (20) and SESSIONS and SHIVE (18) were modified for the determination of ammonium and nitrate nitrogen. STUART's method of preparation was used on 200 cc. aliquots of the alcoholic extract reduced to 50 cc. of cleared extract.

Ammonium nitrogen was determined as described by STUART, except that an aeration period of one and one-half hours was allowed. In addition, the lower ends of the foam traps of test-tubes containing the samples were closed with relatively loose cotton plugs to trap the fine alkaline spray formed during rapid aeration. Determinations checked much more closely when cotton plugs were used

than when they were omitted. This was especially true for the determinations of nitrate nitrogen.

For nitrate nitrogen, the method of SESSIONS and SHIVE was adapted to the Van Slyke-Cullen urea apparatus. Analyses were made on the ammonium-free aliquots. Two cc. of 10 per cent NaOH and about 0.3 gm. of deVarda's alloy were added and aeration carried on at a fairly rapid rate for six hours. In preliminary tests nitrate nitrogen had been quantitatively recovered by this method.

SOLUBLE ORGANIC NITROGEN.—This fraction was calculated as the difference between soluble nitrogen and inorganic nitrogen.

RESIDUAL NITROGEN. The micro-Kjeldahl method outlined by PREGL (14) was used for nitrogen analyses of the alcohol-extracted residues.

Results

VEGETATIVE AND REPRODUCTIVE RESPONSES

Comparative vegetative and reproductive responses of the several series are illustrated in figures 1 and 2. The plants within each series presented a uniform appearance when harvested.

SERIES A: VERY HIGH NITROGEN, NON-FRUITFUL.—The plants in this treatment were dark blue-green in color and grew slowly. The stems were slender and weak, producing few branches. During hot days the leaflets wilted considerably even though completely protected from direct sunlight. Many of the older leaves gradually died from too restricted carbohydrate synthesis. The accumulation of carbohydrates was so limited that eleven of the plants lost practically all their leaves and were removed from the experiment. A large proportion of the leaves on the remaining plants were partially discolored or dead at harvest, thus producing a rather large composite fraction. Root systems, observed at harvest, were markedly limited in extent and lacking in mechanical strength. Despite the extreme nutritional level at which this series was maintained, an average of about one small flower per plant was produced during the course of the experiment. During the period from June 17 to July 18 no flowers were removed. Of the eighteen flowers allowed to remain on the plants, only one gave rise to a gynophore.

SERIES AA: VERY HIGH NITROGEN, LIMITED FRUITFULNESS.—This series resembled series B in general appearance, but branched



FIG. 2.—Plants in the several cultures employed: *AA*, very high nitrogen, limited fruitfulness; *A*, very high nitrogen, non-fruitful; *B*, high nitrogen, limited fruitfulness; *D*, *E*, high carbohydrate.

more freely. In reproductive responses the plants were intermediate between series *A* and *B*, producing an average of 9.6 flowers and 2.3 gynophores per plant.

SERIES B: HIGH NITROGEN, LIMITED FRUITFULNESS.—Plants of this series were much more vegetative than those of series *A*. From June 4, when exfloration was discontinued, they produced an average of 16.5 flowers, 7.6 gynophores, and 0.5 small fruits.

SERIES C: ABUNDANTLY FRUITFUL.—Both vegetative and reproductive responses were greatest in this series. The plants were larger, thicker stemmed than those in all other series, much branched, and almost as blue-green in color as those of the preceding series. They produced an average of 116.8 flowers, 19.6 gynophores, and 28.4 fruits.

SERIES D AND E.—Within two weeks after series *D* and *E* were flushed free from available nitrogen they had become conspicuously light green. A few days later the oldest leaflets became pale along their midribs and larger veins, remaining greenest at their margins. Shortly thereafter those slightly younger underwent

the same color change and the oldest ones turned bright yellow and dropped. Leaves formed after this time were few in number and uniformly pale green in color. In both series the diameters of the

TABLE 6
PERCENTAGE DRY MATTER

PLANT FRACTION	SERIES					
	A	AA	B	C	D	E
Roots.....	7.22	9.02	8.37	9.25	*	9.86
Stems.....	13.70	13.87	16.19	21.81	25.16	26.90
Petioles.....	10.23	10.56	12.37	17.20	17.92	18.58
Leaflets.....	13.33	14.04	15.53	17.38	18.28	18.71
Green gynophores.....				10.53		
Fruits.....				31.60		
Gynophores and fruits.....			16.30			
Composite.....	13.44	12.32	16.54	15.04	21.22	20.63
Tomato stems.....	6.17	*	*	14.98	24.24	19.46

* Soluble solids were lost.

TABLE 7
PERCENTAGE SOLUBLE SOLIDS IN TOTAL SOLIDS

PLANT FRACTION	SERIES					
	A	AA	B	C	D	E
Roots.....	18.85	18.42	19.94	22.43	*	27.19
Stems.....	18.20	17.73	19.23	19.52	14.56	13.95
Petioles.....	31.19	30.07	29.36	25.99	21.20	20.16
Leaflets.....	30.89	27.52	27.56	27.78	26.21	26.62
Green gynophores.....				27.37		
Fruits.....				14.42		
Gynophores and fruits.....			29.23			
Composite.....	30.48	28.61	27.75	31.41	23.33	23.58
Tomato stems.....	39.68	*	*	29.71	19.80	27.54

* Soluble solids were lost.

stems were intermediate between those of plants in series A and C. In general appearance and texture the plants were typically high carbohydrate.

TABLE 8
CARBOHYDRATE AND ETHER EXTRACT FRACTIONS
(PERCENTAGE DRY WEIGHT)

PLANT FRACTION	CHEMICAL FRACTIONS	SERIES					
		A	AA	B	C	D	E
Roots	Total sugars.....	0.06	0.19	2.12	6.50		14.43
	Starch and dextrins...	2.94	2.56	2.68	1.96	(9.85)*	8.37
	Sub-totals.....	3.00	2.75	4.80	8.46		22.80
	Hemicelluloses.....	13.15	13.46	12.81	11.20	(16.84)	11.40
	Totals.....	16.15	16.21	17.61	19.66		34.20
Stems	Reducing sugars.....	None	None	0.20	2.34	1.82	1.35
	Total sugars.....	0.96	1.40	3.33	7.77	5.39	4.85
	Starch and dextrins...	1.53	1.85	3.03	2.09	21.42	28.08
	Sub-totals.....	2.49	3.25	6.36	9.86	26.81	32.93
	Hemicelluloses.....	11.96	12.29	12.35	14.19	11.64	10.44
Petioles	Totals.....	14.45	15.54	18.71	24.05	38.45	43.37
	Total sugars.....	0.28	0.65	1.25	3.11	1.28	1.43
	Starch and dextrins...	3.71	4.61	3.44	2.85	7.06	8.35
	Sub-totals.....	3.99	5.26	4.69	5.96	8.34	9.78
	Hemicelluloses.....	8.49	9.04	8.77	10.61	10.52	11.18
Leaflets	Totals.....	12.48	14.30	13.46	16.57	18.86	20.96
	Total sugars.....	0.02	0.17	0.34	1.15	0.85	1.40
	Starch and dextrins...	1.14	1.51	1.93	4.40	13.42	10.66
	Sub-totals.....	1.16	1.68	2.27	5.55	14.27	12.06
	Hemicelluloses.....	4.28	4.38	4.19	5.20	6.41	5.97
Gynophores and fruits	Totals.....	5.44	6.06	6.46	10.75	20.68	18.03
	Total sugars.....			5.55			
	Starch and dextrins...			8.88			
	Sub-total.....			14.43			
	Hemicelluloses.....			7.03			
Green gyno- phores	Total.....			21.46			
	Ether extract.....			6.28			
	Total sugars.....				2.82		
	Starch and dextrins...				6.04		
	Sub-total.....				8.86		
Fruits	Hemicelluloses.....				9.42		
	Total.....				18.28		
	Ether extract.....				1.63		
	Total sugars.....				6.47		
	Starch and dextrins...				6.80		
Fruits	Sub-total.....				13.36		
	Hemicelluloses.....				4.69		
	Total.....				18.05		
	Ether extract.....				38.56†		

* Percentages in parentheses are calculated on basis of residues of alcoholic extraction.

† Alcoholic soluble extract, 2.95%; alcoholic insoluble extract, 35.61%.

TABLE 8—*Continued*

PLANT FRACTION	CHEMICAL FRACTIONS	SERIES					
		A	AA	B	C	D	E
Composite	Total sugars.....	0.02	0.75	1.10	2.21	2.05	2.14
	Starch and dextrins...	1.85	2.74	2.85	5.90	13.72	14.45
	Sub-totals.....	1.87	3.49	3.95	8.11	15.77	16.59
	Hemicelluloses.....	5.70	5.85	6.44	7.56	7.48	5.54
	Totals.....	7.57	9.34	10.39	15.67	23.25	22.13
Tomato stems	Total sugars.....	0.85			20.46	12.34	17.70
	Starch and dextrins...	3.15		(3.22)	9.24	15.76	21.55
	Sub-totals.....	4.00			29.70	28.10	39.25
	Hemicelluloses.....	8.68		(15.83)	11.75	13.18	11.94
	Totals.....	12.68			41.45	41.28	51.19

SERIES D: HIGH CARBOHYDRATE, GYNOPHORE-PRODUCING.—These plants were identical in appearance with those of series E until about eight days after the first addition of $\text{Ca}(\text{NO}_3)_2$ to their nutrient solution. During the remainder of the experiment, the first three weeks of July, a few new leaves appeared and the plants as a whole became slightly greener. No nodules were visible at harvest on any of the high carbohydrate plants, except for a few small ones near the hypocotyl of a single plant.

For the period during which flowers were no longer removed until the application of $\text{Ca}(\text{NO}_3)_2$ caused an increase in blooming (June 6 to July 1), the plants produced an average of 6.8 flowers; during the remainder of growth (July 2–18) the average was 10.3 flowers. Only one gynophore had been produced by June 18, a total of twenty by July 4, and of twenty-three by July 20 by the forty-eight plants in this series. Enlargement of ovaries was scarcely perceptible.

SERIES E: VERY HIGH CARBOHYDRATE, NON-FRUITFUL.—From July 5 to 18 no blossoms were removed from the plants of this series. An average of 4.1 flowers was produced per plant. Only one plant in the entire lot developed a gynophore.

COMPARATIVE CULTURES OF TOMATO.—Although the vegetative responses of tomatoes were similar to those of peanuts, reproductive behavior was quite different. Tomato plants of series A were moderately vegetative, medium green in color, and very succulent. During the period of much reduced illumination in the earlier part of

TABLE 9
NITROGEN FRACTIONS (PERCENTAGE DRY WEIGHT)

PLANT FRACTION	CHEMICAL FRACTIONS	SERIES					
		A	AA	B	C	D	E
Roots	Ammonium N	0.113	0.276	0.035	0.025		None
	Nitrate N	0.130	0.190	0.310	0.040		None
	Soluble organic N	0.673	0.395	0.218	0.146		0.007
	Residual N	1.913	1.880	1.571	1.638	(1.003)	0.886
	Total N	2.829	2.741	2.134	1.849		0.893
Stems	Ammonium N	0.067	0.049	0.025	0.009	None	None
	Nitrate N	0.470	0.610	1.010	0.060	None	None
	Soluble organic N	1.086	0.568	0.233	0.087	0.069	0.065
	Residual N	1.143	1.102	1.022	0.645	0.357	0.326
	Total N	2.766	2.329	2.290	0.801	0.426	0.391
Petioles	Ammonium N	0.096	0.048	0.042	0.027	None	None
	Nitrate N	0.990	1.120	1.060	0.110	None	None
	Soluble organic N	1.240	0.490	0.817	0.096	0.117	0.094
	Residual N	1.845	1.599	1.606	0.874	0.602	0.555
	Total N	4.171	3.257	3.525	1.107	0.719	0.649
Leaflets	Ammonium N	0.100	0.049	0.046		None	None
	Nitrate N	0.280	0.310	0.460	0.367	None	None
	Soluble organic N	1.320	0.563	0.629		0.195	0.179
	Residual N	4.717	4.447	4.426	3.130	1.114	1.205
	Total N	6.417	5.369	5.561	3.497	1.309	1.384
Gynophores and fruits	Ammonium N			0.010			
	Nitrate N			0.390			
	Soluble organic N			1.188			
	Residual N			2.839			
	Total N			4.411			
Green gynophores	Ammonium N				0.030		
	Nitrate N				0.110		
	Soluble organic N				1.143		
	Residual N				1.721		
	Total N				3.004		
Fruits	Ammonium N				0.015		
	Nitrate N				0.020		
	Soluble organic N				0.160		
	Residual N				2.327		
	Total N				2.522		
Composite	Ammonium N	0.174	0.073	0.055	0.044	None	None
	Nitrate N	0.290	0.280	0.720	0.100	None	None
	Soluble organic N	1.470	0.763	0.517	0.367	0.257	0.221
	Residual N	3.162	3.033	2.760	2.912	1.127	1.034
	Total N	5.096	4.149	4.824	3.423	1.384	1.255

TABLE 9—*Continued*

PLANT FRACTION	CHEMICAL FRACTIONS	SERIES					
		A	AA	B	C	D	E
Tomato stems	Ammonium N	1.259			0.262	None	None
	Nitrate N	0.820			0.040	None	None
	Soluble organic N	2.116			0.707	0.201	0.221
	Residual N	1.163		(1.258)	0.853	0.500	0.421
	Total N	5.358			1.862	0.701	0.642

the experiment, they developed two to three flower buds per cluster, which remained very small and eventually dried and fell off. Later light intensity was slightly increased and the buds formed were larger and persistent. The series B plants were vigorously vegetative, dark green in color, succulent, and but sparingly branched. They produced clusters of large flowers which fell shortly after opening. Even though the plants of series C did not grow so tall as those of series B, they were profusely branched and bore a relative abundance of flowers and fruits. Series D and E were almost identical in general appearance, growing very little and becoming yellowish and woody. The flower buds of series D, however, were slightly larger than those of series E. One plant of series E blossomed, bore one small fruit and died.

CHEMICAL DATA

Data of percentage dry matter are given in table 6, of percentage soluble solids in total solids in table 7, of carbohydrate and ether extract analyses in table 8, and of nitrogen fractions in table 9.

Discussion

FLOWER-TO-GYNOPHORE INTERVAL

It is apparent that the enlargement of fruits noticeably increased the average flower-to-gynophore interval but did not change the mode of this interval.

In certain preliminary experiments it had been observed that the average time required for the appearance of the first gynophore on a plant was about one week after its flower had opened. The enlargement of fruits, however, was found to increase the average interval

approximately 50 per cent, as shown by the data for July 16 to 31 in table 1. The records in this table are for plants which had commenced to bloom about June 14, so that fruit enlargement was in progress when the first flowers were tagged for a study of the interval. The period between the opening of flowers and the appearance of gynophores became shorter again during August, because most of the gynophores produced during July and August arose from stems which drooped over the rims of the jars and consequently did not set fruits.

When the data are analyzed on the basis of statistical modes, there appears to be a much greater degree of stability for the period between anthesis and the initiation of meristematic activity in the gynophore than the data of averages indicate. Table 1 shows that (1) within each series the statistical mode of this period was not altered by the onset of fruit development, having maintained itself at seven days in the high nitrogen series and at nine days in each of the other three series throughout the period of observation; and (2) with the possible exception of the high nitrogen series, there was no correlation between the mode of the interval and the amount of nitrate supplied.

BEHAVIOR OF VERY LOW NITROGEN PLANTS.—From the preceding comments on modal stability, it is evident that, for plants producing gynophores, the general level of nutrition has but little influence on the rate of their appearance. If very low nitrogen plants bearing gynophores and fruits have their supply of available nitrogen sufficiently reduced, however, the nutritional level of such plants will fall below the threshold of meristematic activity in the gynophore initials. This change occurred in the very low nitrogen plants as recorded in table 1. Until August 1 they produced gynophores with a modal frequency equal to that of the medium nitrogen series; but after August 1 they developed no gynophores at all, although they continued to bloom sparingly.

The response of the plants in series D is also significant in this respect. They were below the threshold of gynophore production when the application of minute quantities of nitrate was started on June 22. By July 4 the forty-eight plants in the series had produced a total of twenty gynophores; but only three additional gynophores

had formed by July 20, although the intermittent application of nitrate was continued until that date. These responses indicate that the nutritional level of most of the plants was raised above the threshold of gynophore initiation for a period of not more than twelve days (from June 22 to July 4), and that the extension of gynophores soon caused the nutritional level to drop again below that threshold.

PRECOCITY OF GYNOPHORE DEVELOPMENT.—Correlation of the preceding observations indicates a definite precocity of gynophore development for plants representing a wide range of nutritional levels; that is, if gynophores are formed at all, the modal frequency of their flower-to-gynophore intervals will be confined to a very narrow range not exceeding a period of nine days.

Lack of sufficient data makes it impossible to extend the application of this concept to very high nitrogen plants such as those of series A and B.

RELATIVE REPRODUCTIVITY OF SERIES B AND C

The data given under "Vegetative and reproductive responses" for the fruiting behavior of series B are apt to be misleading, as they are based on the numbers of gynophores and fruits. Data comparing average weights of these plant parts with those of series C are significant. On a green weight basis the average weights of non-fruiting (green) gynophores in series B and C were 0.06 and 0.13 gm. respectively, and of fruits 0.4 and 1.02 gm. As each plant of series B produced an average of only 0.2 gm. of fruit and each one of series C an average of 29.02 gm., the former may be considered relatively non-fruitful.

STABILITY OF REPRODUCTIVE FUNCTION

In this discussion of stability emphasis is placed on the opening of flower buds and the initial stages of fruit formation. These two phases of reproduction are less readily modified in the peanut plant than in the tomato, and may be summarized as follows. In series A (very high nitrogen) the peanut bloomed sparingly and was non-fruitful, but the tomato failed even to open flower buds. In series B (high nitrogen) the peanut produced many flowers and a few small fruits, while the tomato blossomed and remained entirely non-fruitful. In series D (high carbohydrate) the peanut bore numerous

flowers and a few gynophores, but the tomato gave rise to flower buds only. In series E (very high carbohydrate) the peanut blossomed freely and was non-fruitful, while reproduction in the tomato was limited to the formation of a few small flower buds. These results show that the reproductive function is more readily suppressed in the tomato than in the peanut.

GENERAL TRENDS OF CHEMICAL DATA

Table 6 shows a consistent increase in the percentage dry matter from highest nitrogen to highest carbohydrate series for all plant fractions except the composites of series A and B. The latter are relatively high in percentage dry matter, largely because the leaflets included had a higher proportion of discolored and partially desiccated tissue.

The percentage of soluble solids in total solids tends to decrease from highest nitrogen to highest carbohydrate series, with the notable exception of the root fractions, which have an inverse correlation.

The following trends are evident in tables 8 and 9. From highest nitrogen to highest carbohydrate series soluble and residual nitrogen decrease and total carbohydrates increase. These trends agree with those of investigations on other species not conditioned by photoperiodic behavior or by specific temperature treatments.

There is no uniformity of opinion as regards the relative importance of the several carbohydrate and nitrogen fractions in their relations to vegetation and reproduction of plants (5, 8). Lack of concordance in viewpoints is in part associated with differences inherent in the plants which have been studied. Some of them are normally annual; many are herbaceous but potentially perennial; others are woody perennials which have alternate periods of dormancy and growth (13, 20), and which may be subject to cumulative effects at present undefined. In photoperiodic response they represent short day plants, indeterminate bloomers, and those which flower only under long day conditions (10). Many plants are characterized by asexual storage organs, the enlargement of which may modify the interpretation of chemical data. Certain plants are highly sensitive to range of temperature (11, 24, 25). Because of these and other in-

herent differences, it is to be anticipated that the vegetative and reproductive responses will not always be correlated with exactly the same chemical fractions.

Most of the factors specifically mentioned in the preceding discussion were not limiting in the present study of the peanut. It is neither an annual plant nor one sufficiently hardy to exhibit the growth rhythm of a woody perennial, but continues to fruit indefinitely under certain conditions. It has proved to be an indeterminate bloomer. None of its asexual parts become especially enlarged for food storage. When given an adequate supply of water and mineral salts, it grew luxuriantly under the conditions of temperature prevailing during the period of experimentation.

The significant chemical fractions in the peanut plant are considered to be (1) total sugars, starch, and dextrans taken as a unit; and (2) total nitrogen.

CARBOHYDRATE FRACTIONS.—In correlating chemical data in nutritional studies, such as the one reported here, it seems logical to include only those chemical fractions which correspond to the vegetative and reproductive responses obtained. On this basis total sugars, starch, and dextrans (table 8) considered together are the significant carbohydrates; for neither total sugars alone nor starch and dextrans alone are consistently correlated with the responses observed. Although "hemicelluloses" were determined on all plant fractions, their ranges in percentage from highest to lowest nitrogen series were much too small to regard this chemical fraction of any importance in the peanut.

NITROGEN FRACTIONS.—The choice of significant nitrogen fractions was not restricted to the preceding basis of correlation. Although the determinations for residual and soluble organic nitrogen (table 9) correspond, on the whole, to the nutritional levels of their respective cultural treatments, those of the inorganic forms do not. On the basis of correlation alone, only the assimilated nitrogen should be used for interpretive purposes. The inorganic fractions are included in the interpretation presented because they aid in maintaining metabolic processes at approximately a given level. A common case in point is that of a medium nitrogen plant growing under conditions favorable to carbohydrate synthesis. So long as such a

plant is given an adequate supply of inorganic nitrogen its nutritional level will undergo little change. But if the plant is suddenly deprived of all externally available nitrogen, it soon becomes high carbohydrate. A progressive change in its nutritional level occurs as the inorganic nitrogen in its tissues becomes metabolized without being replaced by absorption from the soil solution. Even though the inorganic nitrogen fractions in plant tissues may at times be present in excess of immediate needs for maintenance of a nutritional level, at least part of such nitrogen functions in this manner in intermediate bloomers.

The influence of inorganic nitrogen in plant tissues on the principal phases of carbohydrate metabolism is a relatively new field of investigation. HAMNER (3) has recently reported that nitrates have a direct influence on the rate of respiration in wheat. The effects of inorganic nitrogen on photosynthesis need careful study.

In view of the preceding contingencies, total nitrogen, rather than any specific nitrogen fraction, should be used in correlating nutritional studies of the peanut and of other plants of similar physiological constitution.

INTER-SPECIAL CORRELATION OF CHEMICAL DATA.—When the analyses for tomato and peanut stems from any specific cultural treatment are compared, two correlations appear. Data in table 9 show that, within each cultural treatment, the tomato maintained approximately twice the concentration of total nitrogen found in the peanut. On the other hand, no such consistent inter-special correlation exists in the data for carbohydrates (table 8). Accordingly when the two species are considered together, nutritional levels are more closely associated with the nitrogen than with the carbohydrate fraction.

CORRELATION OF VEGETATION AND REPRODUCTION

In the five main cultural treatments, vegetative activity increased from very high nitrogen to abundantly fruitful plants and decreased from the latter to very high carbohydrate plants. Gynophore and fruit production followed similar quantitative changes. The setting and enlargement of fruits did not obviously retard the rate of vegetative extension of the fruitful plants in series C. For the peanut,

then, vegetation and reproduction are not opposing tendencies, but are complements in the course of development. This is true also for the tomato (5).

MISCELLANEOUS OBSERVATIONS

A few grams of coarsely ground seed of the high and very low nitrogen series of 1933 have been kept in 250 cc. bottles since the time of harvest. In less than a year the high nitrogen sample had become rancid in odor and taste, but the very low nitrogen sample was still free from rancidity after a period of three years. The seed of the high nitrogen series (1933) had slightly less ether extract than that of the very low nitrogen series (table 3).

A distinct gradation of pigmentation in seed coats was observed throughout the four series grown in 1933. The seed coat color of the highest nitrogen series was the usual rich brown, that of the very low nitrogen culture was pale and almost pink in color. If the color of the seed coat is to be employed in the classification of varieties (19), it will be necessary to grow all the plants under the same environmental conditions.

As the plants in series D and E approached the high carbohydrate condition, the new leaflets were observed to have numerous marginal hairs or trichomes. At the time most of these plants were harvested, a jar of six plants was given an abundance of available nitrogen and placed in the shade. Leaf primordia formed after the resumption of growth produced smooth-margined leaflets only. The test was repeated on other high carbohydrate plants with the same results. The culture of six plants of series E was modified by giving them an excess of the chloride ion for a period of forty days. One result of this modification was the almost complete disappearance of starch from the stems. When these plants were abundantly supplied with nitrogen even the first leaflets to expand were free from marginal ciliation. Leaflets of high nitrogen plants (series A, AA, and B) were smooth-margined, and those of series C bore scattered hairs much less conspicuous than those of series D and E. These results indicate that the growth of marginal hairs is associated with a relatively high carbohydrate level of metabolism.

Summary

1. In the peanut plant, greatest vegetative extension and fruitfulness occurred in the same cultural treatment.
2. All high nitrogen plants were dark blue-green in color, slender stemmed and succulent; all high carbohydrate plants were very pale yellow-green, relatively thick stemmed, and firm in texture. Both were weakly vegetative and non-fruitful.
3. From highest nitrogen to highest carbohydrate series the percentage dry matter and total carbohydrates increased, and the percentage soluble solids and total nitrogen decreased consistently with vegetative and reproductive responses. The root fractions increased in percentage soluble solids.
4. "Hemicelluloses" were not correlated with levels of nutrition.
5. The high carbohydrate condition favored a slightly greater percentage of ether extract in the seeds and gynophores, the suppression of rancidity in the seeds, and the development of marginal hairs on the leaflets.
6. Gynophore development was precocious. The mode of the flower-to-gynophore interval was only slightly influenced by the enlargement of fruits on older gynophores or by extensive variations in metabolic levels, but elongation of the gynophores was abruptly inhibited by extreme levels of nutrition.
7. The fruiting tendency was less sensitive to nutritional change in the peanut than in the tomato.
8. The concentration of the phosphate ion in nutrient solutions must be greatly reduced to obviate injury when the peanut plant is grown in the light.
9. Ammonium nitrogen nutrient solutions which do not precipitate when applied at pH 7.1 are reported.
10. A method for determining nitrates by a six-hour aeration period is described.

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